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What makes a nest-building male successful? Male behavior and female care in penduline tits

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Why do females increase parental effort when caring for the offspring of attractive males? First, attractive males may be poor fathers so that their females are compelled to increase their own contribution in order to fledge some young (the partner-compensation hypothesis). Second, females mated to attractive males may be willing to increase their parental effort to reap high indirect benefits for their offspring, and in turn males can decrease their own contribution (the differential allocation hypothesis [DAH]). We investigated these hypotheses in the penduline tit *Remiz pendulinus*, a small passerine bird that has sequential polygamy by both sexes and strict uniparental care either by the male or the female. We focused on two sexually selected male traits: nest size and nest-building behavior. We show that male care is unrelated to nest-building behavior, whereas females are more likely to care for the offspring of those males that spend more time nest building. Females also more likely care for the offspring of males that build large nests. Consequently, the reproductive success of males increases with nest size and nest-building behavior. Our results are consistent with the DAH and suggest that nest-building behavior and nest size are under postmating sexual selection in penduline tits. *Key words:* differential allocation, nest building, parental care, penduline tit, reproductive success, sexual selection. *[Behav Ecol 16:994–1000 (2005)]*

Secondary sexual characters of males often evolve through female mate choice (premating sexual selection; reviewed by Andersson, 1994) when females prefer certain male traits, and males bearing those traits obtain higher mating success than males without them. Some male traits, however, not only influence the premating attractiveness of males but also the parental investment of both males and females, affecting male reproductive success (Houston et al., 2005; Limbourg et al., 2004; Møller and Jennions, 2001).

On the one hand, males bearing certain traits may reduce their own care because females find them attractive (Møller and Thornhill, 1998). Attractive males may invest more time in seeking out and attracting new mates, trading off parental effort against mating effort (Houston et al., 2005; Kokko, 1998; Magrath and Komdeur, 2003). Due to reduced male care, females mated to attractive males are compelled to elevate the level of their own care to achieve some reproductive success (partner-compensation hypothesis, PCH; Witte, 1995; Wright and Cuthill, 1992). On the other hand, females may increase their parental effort by preferentially investing in the offspring of attractive males (differential allocation hypothesis, DAH; Burley, 1986). The DAH postulates that mates of attractive males should gain higher than average direct (e.g., good territory) or indirect (e.g., attractive offspring) benefits (Sheldon, 2000). Therefore, it would be worthwhile for females paired to attractive mates to invest more in caring for their young. In response to such elevated female care, males may (or may not) decrease their own level of parental care (Dearborn, 2001; Freeman-Gallant, 1998).

Both the PCH and the DAH predict that females will increase their parental effort if they are mated to attractive males. However, they can be separated if (1) the sequence of the decisions is known because the PCH predicts that the male decides first, whereas the DAH predicts that the female decides first or (2) males do not respond to the elevated female investment as this is inconsistent with the PCH. Several studies have shown that females mated to attractive males did indeed increase their clutch size, egg size, or the testosterone content of their eggs (e.g., Cunningham and Russell, 2000; Gil et al., 1999; Komdeur et al., 2005; Petrie and Williams, 1993; reviewed by Sheldon, 2000). However, to our knowledge no study has yet demonstrated that females of biparental species (or in which both the male and the female may care) enhance their parental effort in response to male attractiveness independently from the male's effort. It is especially important to disentangle male and female parental decisions in relation to male attractiveness and to test the PCH and the DAH because they have different implications for sexual selection. While the DAH suggests that there is postmating selection on male traits that magnifies the effect of premating sexual selection, the PCH does not invoke such a mechanism (Møller and Thornhill, 1998).

The objective of our study was to investigate how nest-building behavior and nest size influence parental care by the male and the female and the outcomes for male reproductive success. We also investigate whether the relationships between male traits and reproductive success are more consistent with the PCH or the DAH. We studied the penduline tit *Remiz pendulinus*, a small Eurasian passerine bird, which has a diverse breeding system that allowed us to tease apart male and female parental decisions.

In the penduline tit, both the male and the female may desert the clutch, and the offspring are raised exclusively by a single parent (male care: 5–20% of clutches, female care: 50–70% of clutches). In all populations that have been studied to date, about 30–40% of clutches are deserted by both parents before incubation commences (Franz, 1991; Franz and Theiss, 1983; Persson and Öhrström, 1989; Szentirmai I and Székely T, unpublished data). Although the sequence of

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parental decisions is not known (van Dijk RE, Szentirmai I, Komdeur J, and Székely T, unpublished data), the occurrence of biparental desertion suggests that the decision of one parent does not necessarily determine the decision of the other, that is, if the male deserts, females do not necessarily care or vice versa. Male penduline tits build complex domed nests to attract females. Males that have large nests are more likely to mate and also mate earlier than males with small nests (Hoi et al., 1994; Schleicher et al., 1996). Larger nests appear to provide direct benefits because large nests have better insulative capacity and thus reduce the temperature fluctuations of eggs and promote embryonic development (Grubbauer and Hoi, 1996; Hoi et al., 1994; Williams, 1996). The majority of nest building is carried out by the male, and although females also contribute to nest building near the end of building, they have no significant effect on nest size (Hoi et al., 1994; see also Methods). Both nest-building behavior and nest size are repeatable over a breeding season, suggesting that male nest-building behavior and nest size are consistent traits of a given male (Pogány Á, Szentirmai I, and Székely T, unpublished data). In addition, nest building is time and energy consuming, thus nest-building behavior is likely to convey information on either male or nest-site quality (Berg et al., 2005; Bleeker et al., 2005; Franz and Theiss, 1983). As such, nest-building behavior and nest size may be viewed as part of the extended phenotype of the male (Dawkins, 1982). Although nest-building behavior has not been investigated in penduline tits (apart from our work presented here), it has been shown to influence both male mating success and female parental investment in several bird species (Evans, 1997; Moreno et al., 1994; Soler et al., 1998; reviewed by Collias NE and Collias EC, 1984; Hansell, 2000).

To tease apart whether nest-building behavior and nest size influence the parental decision (care or desert) of males and females, we tested two predictions. First, if nest-building behavior and nest size influence male parental decision, then PCH predicts that male care should be negatively and female care should be positively related to nest-building behavior and nest size. Second, if nest-building behavior and nest size influence female parental decision, then DAH predicts that female care should be positively related to nest-building behavior and nest size, whereas male care is not expected to be associated with nest building and nest size.

METHODS

Fieldwork

We investigated penduline tits at Fehértó, South Hungary (46° 19′ N, 20° 5′ E), in 2002 (5 April–2 August) and 2003 (15 April–22 August). Fehértó is an intensively used fishpond system (1321 ha) consisting of 16 fishpond units, which are separated by dykes. Approximately 90 male and 50 female penduline tits breed on the dykes of our study site on mostly willow (*Salix* spp.) and poplar (*Populus* spp.) trees.

We searched for nests and unmated males nearly every day. We investigated nest-building behavior of males, and we investigated nest size at 184 nests (2002, 43 nests; 2003, 141 nests). Of these nests, 26 were found ("found date") on the first day of nest building (stage A; when only a small amount of nest material is woven around a twig fork, see Cramp et al., 1993: Figure B on page 385), and thus, their date of initiation was known. The initiation dates of those nests that were found in later stages (stages B–E; see Cramp et al., 1993: Figure C–I on pages 386–387) were estimated using the progress of nest building at those nests that were found at initiation ($N = 46$ for the total population) separately for each stage. The mean age of nests in stage B was 2 days, and it did not vary throughout the breeding season; therefore, we calculated their nest initiation date as found date − 2 days. For nests in stages C–E, quadratic relationships between the mean ages of nests and nest initiation date provided better fits than linear ones: stage C, nest age = $3.882 + 0.119 \times$ found date − $0.000899 \times$ (found date)^2; stage D, nest age = $-23.962 + 0.805 \times$ found date − $0.00429 \times$ (found date)^2; and stage E, nest age = $-96.268 + 2.368 \times$ found date − $0.0117 \times$ (found date)^2.

Females and males were caught either by mist nets and playbacks or by trapping the incubating parent in the nest. Penduline tits have sexually dimorphic plumage that allows unambiguous sexing of adult breeders because males have wider masks than females (Cramp et al., 1993) and they have more intense rusty patches on their breast (Szentirmai I, personal observation). Males were caught and individually color ringed at 156 of 184 nests (85%), and females were caught and individually color ringed at 59 nests (45% of mated nests). Unmated males were visited for 15 min every other day until they found a mate. Mated males were recognized by copulating with a female and/or building the nest together with a female. At 131 of the 184 nests, males attracted a female and eggs were laid. We knew the identity of mated males at 103 nests, and these were built by 66 different males. Mated pairs were also visited for 15 min every other day until one parent (or both) deserted the clutch or until offspring fledged. Desertion was recognized if one or both parents were not seen at the nest for at least two consecutive nest checks. Postdesertion nest checks at 49 nests confirmed that desertion was permanent at all 49 nests.

We observed the building behavior of individually marked unmated males in 2003. Behavioral observations were carried out two to four times on different days for 30 min each using binoculars from a blind 15–20 m from the nest. An equal number of observations were attempted in the morning (0006 to 0012 h local time, Central European Time) and in the afternoon (0015 to 0019 h) to control for possible time effects. Male behavior was recorded every 20 s. Between scans, we noted the number of times he carried nest material to the nest. Nest building was defined as weaving nest material into the nest or piercing the nest with the bill. From these behavioral observations, we calculated mean nest building time (percent time spent on nest building) and the carrying frequency (frequency of carrying nest material to the nest) for each male during 30 min of observation.

Nest size (height, thickness, and volume) was measured 6–9 days after the start of incubation. We did not measure nest size during egg laying or early incubation to avoid disturbance that may potentially cause clutch desertion. Because biparentally deserted nests are incomplete and their sizes are not comparable to that of nondeserted nests (Persson and Öhrström, 1989; Szentirmai I, unpublished data), we restricted our analyses to complete nests that were incubated by either the male or the female. Nest height was measured as the maximum external height of the nest (±0.5 cm), and nest volume was measured by filling the nest with plastic beads (diameter about 4 mm) and then pouring the beads into a 500-cm^3 graduated cylinder (±1 cm^3). Nest thickness was measured by a sliding caliper (±1 mm) in the middle of the nest bottom. Eggs were removed from the nest during the measurements. Because females also contribute to nest building, their behavior may potentially confound the analyses of nest size and male building effort. However, using a subset of nests where we also recorded the building behavior of females ($N = 6$ females), we found that their nest-building time and carrying frequency were unrelated to the final nest size (Spearman rank correlations: $r_{smin} = -.522$, $r_{smax} = .400$,

$N = 6$ females, $p > .28$, for correlations with nest height, volume, or thickness).

Clutch size was determined 6–9 days after the start of incubation, except if both parents deserted, when the clutch size was determined at the time of biparental desertion. Nestlings were counted on the expected day of hatching (14 days after the start of incubation, Cramp et al., 1993), and on one or two consecutive days until the last egg hatched (eggs usually hatch within 3 days). In the analyses, the total number of hatched nestlings was used, and hatching success was defined as the proportion of eggs that hatched. The number of fledglings was counted 21–22 days after the last nestling hatched, and fledging success was defined as the proportion of nestlings that fledged.

Data processing and statistical analyses

We had data on nest size from multiple nests of only 10 out of 66 males (15.2%) and from multiple nests on nest-building behavior of 26 out of 66 males (39.4%); therefore, to maximize sample size, we selected one nest for each male for analysis (see exceptions below). For each male, we chose the nest that provided the most complete data set (nest size, nest building, parental care, and reproductive success) and thus analyzed nest size and building behavior at 46 nests. Those analyses in which more than one nest may be used per male are indicated in the description. Carrying frequency was not normally distributed, so we used nonparametric statistics for this variable.

Parental decisions (i.e., care/desert the clutch) were analyzed in two ways. First, we chose one nest per male and used binary logistic regressions with backward elimination to investigate the parental decision of the male or the female with regard to male building behavior and nest size. In the analyses of nest size, biparentally deserted nests were not included (see above). Second, we calculated the proportion of each male's clutches that were deserted by the male over the full breeding season and related it to the mean nest-building times, carrying frequencies, and nest sizes of the male. Similarly, we calculated the proportion of each male's clutches that were cared for by their mates and related it to the mean of nest-building times, carrying frequencies, and nest sizes of the male. In all analyses of parental care, we controlled for nest initiation date because previous studies indicated that parental decisions may change over the breeding season (Persson and Öhrström, 1989).

Reproductive success was also analyzed in two ways. First, we chose a single nest per male and related the number of nestlings, the number of fledglings, hatching success, and fledging success to nest-building time, carrying frequency, and nest size. Because previous studies indicated that reproductive success of nests with female-only care and male-only care was different, we only analyzed clutches with female-only care (Szentirmai I, Székely T, and Komdeur J, unpublished data). As sample sizes were small, we calculated the statistical power of these correlations (Cohen, 1988). Second, we calculated the total number of fledglings produced by males over a breeding season in their nests (male reproductive success) and related it to the mean of nest-building times, carrying frequencies, and nest sizes. We acknowledge that reproductive success might be different using genetic data (we are currently fingerprinting the families), although the single study on parentage of penduline tits found low extrapair paternity (6.9% of young; Schleicher et al., 1997). If data were available for a male in both years, we analyzed only his data from 2003 because behavioral data were only available from this year. We used nonparametric correlations to analyze all variables of reproductive success as they were not normally distributed.

We used SPSS 11 (SPSS Inc., Chicago, Illinois, USA) for statistical analyses and provide two-tailed probabilities. The null hypothesis was rejected at $p < .05$.

RESULTS

Correlates of nest-building behavior and nest size

Nest-building time and carrying frequency were unrelated to each other ($r_s = .058$, df = 43, $p = .70$). Nest-building time was unrelated to nest age (Pearson correlation: $r_p = .022$, $N = 46$, $p = .88$), although carrying frequency decreased with nest age (Spearman rank correlation: $r_s = -.428$, $N = 46$, $p = .003$). Therefore, we adopted a conservative approach and controlled for nest age statistically in all analyses of both nest-building time and carrying frequency.

Some nest size variables were correlated with each other (height and thickness: $r_p = .642$, $N = 45$, $p < .001$; height and volume: $r_p = .296$, $N = 45$, $p = .048$; thickness and volume: $r_p = .038$, $N = 44$, $p = .80$); therefore, we used multivariate analyses in which height, thickness, and volume were the response variables. Nest size was related neither to nest-building time nor carrying frequency (multivariate analyses of variance, MANOVA—nest-building time: Wilks's Lambda = 0.928, $F_{3,17} = 0.436$, $p = .73$; carrying frequency: Wilks's Lambda = 0.934, $F_{3,17} = 0.403$, $p = .75$; nest age: Wilks's Lambda = 0.953, $F_{3,17} = 0.436$, $p = .84$).

Nest size decreased with nest initiation date (Figure 1, MANOVA: Wilks's Lambda = 0.646, $F_{3,38} = 6.954$, $p = .001$). The seasonal decline may emerge in two ways. First, each male may build smaller and thinner nests over the breeding season. Our data are partially consistent with this suggestion because the volume of the first nest of a male was larger than the volume of his last nest in the same breeding season (paired t tests—volume: $t_9 = 2.345$, $p = .044$; height: $t_{10} = 1.204$, $p = .25$; thickness: $t_{10} = 1.281$, $p = .22$). Second, males that arrive late at the study site may build smaller nests than early-arriving males. Our data are partially consistent with this latter suggestion as well because nest height and thickness decreased with the initiation date of the first nest of the males (MANOVA—overall effect: Wilks's Lambda = 0.784, $F_{3,36} = 3.298$, $p = .031$; height: $F_{1,38} = 6.285$, $p = .017$; thickness: $F_{1,38} = 7.926$, $p = .008$; volume: $F_{1,38} = 2.821$, $p = .10$). Because nest size changed over the breeding season, we included nest initiation date as a covariate in analyses of nest size.

Parental decisions

Of the 46 clutches at which we investigated nest-building behavior, 19 were cared for by females, 9 by males, and 18 were deserted biparentally. Females were more likely to care for the clutches of those males that spent more time on nest building (Figure 2A, Table 1). Accordingly, the proportion of the clutches of each male that were cared for by females increased with male nest-building time (partial rank correlations controlling for nest age and nest initiation: $r = .350$, df = 40, $p = .023$). In contrast, parental decision of males was unrelated to their own nest-building time (Figure 2A, Table 1), and the proportion of their clutches that they deserted was not related to their nest-building time ($r = .044$, df = 40, $p = .78$). Neither female nor male parental decisions were related significantly to carrying frequency (Table 1). Similarly, the proportion of clutches cared for by the female and the proportion of clutches deserted by the male were also unrelated to carrying frequency (partial rank correlations controlling for nest age and nest initiation—female care: $r = .181$, df = 40, $p = .25$; male desertion: $r = .056$, df = 40, $p = .73$).

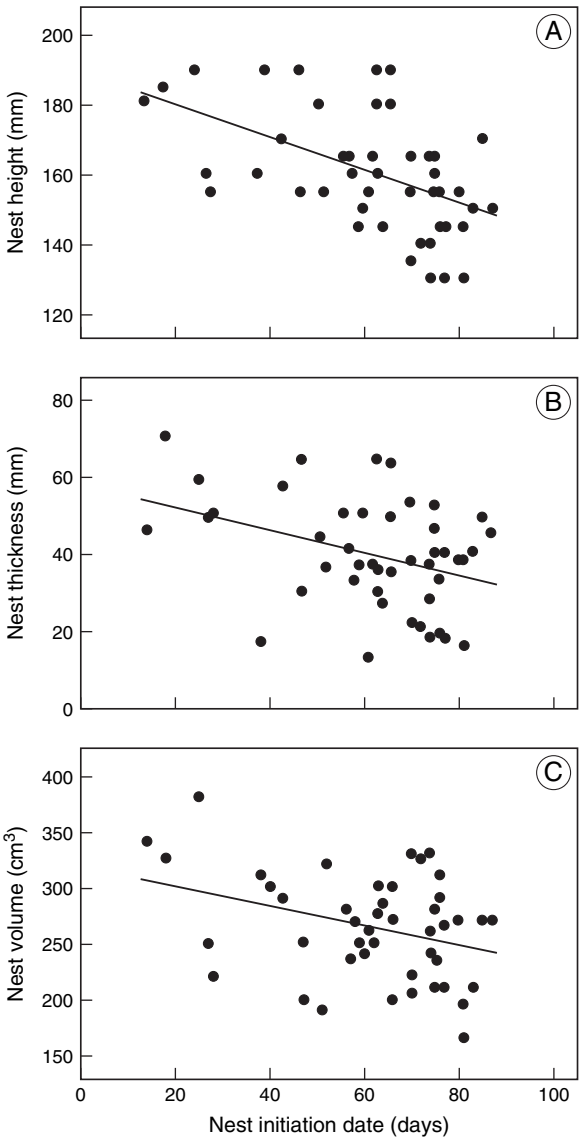

Figure 1
Three measures of nest size of penduline tits in relation to nest initiation date: (A) height (MANOVA: $F_{1,40} = 17.480$, $p < .001$), (B) thickness ($F_{1,40} = 10.591$, $p = .002$), and (C) nest volume ($F_{1,40} = 4.454$, $p = .041$). Day 0 is set to the date when the first nest was initiated in the breeding season (3 April 2002 and 13 April 2003).

Of the clutches at which we investigated nest size, 34 and 12 out of 46 were cared for by the female or the male, respectively (biparentally deserted clutches were not included, see Methods). Both nest height and volume were related significantly to parental decisions, with tall and voluminous nests more likely to be cared for by the female and deserted by the male than small nests (Figure 3, Table 2). Nest thickness was also marginally significantly related to parental decisions (Table 2). The proportion of a male's clutches that were cared for by their females increased with nest size (partial rank correlations controlling for nest initiation—nest height: $r = .372$, df = 37, $p = .020$; nest volume: $r = .533$, df = 29, $p = .002$; thickness: $r = .067$, df = 29, $p = .72$). Similarly, the proportion of clutches deserted by the male tended to increase with nest size (height: $r = .364$, df = 37, $p = .023$; volume: $r = .331$, df = 29, $p = .069$; thickness: $r = -.177$, df = 29, $p = .34$).

Male parental decisions were also related to nest initiation date, with males more likely to care for clutches if they initiated their nests late in the breeding season (Figure 2B, Table 1). Female parental decisions were unrelated to nest initiation date (Figure 2B, Table 1).

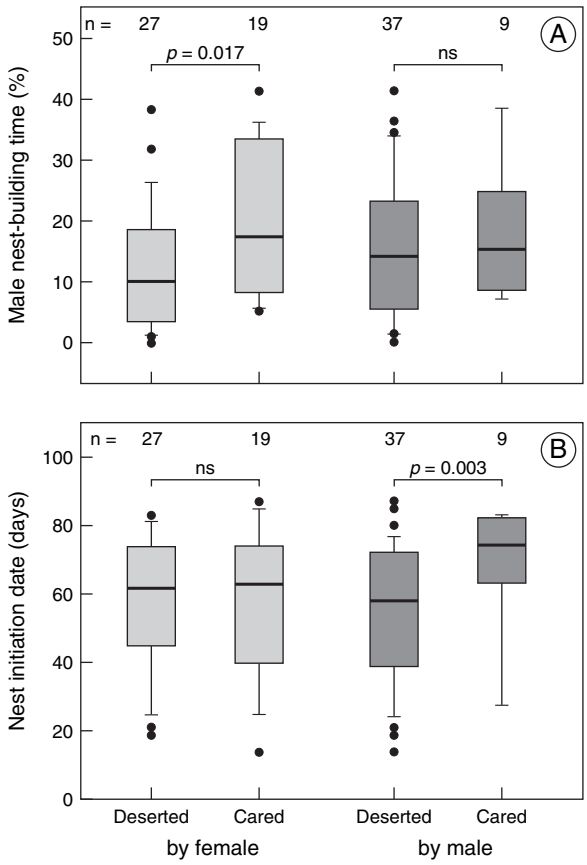

Figure 2
Parental care decisions of females (light gray boxes) and males (dark gray boxes, see also Table 1) in relation to (A) nest-building time and (B) nest initiation date. The lines in the boxes are drawn across the median, and the bottom and the top of the boxes are the lower and upper quartiles, respectively. Lower and upper whiskers represent 10th and 90th percentiles, respectively, and dots indicate outliers. Numbers above the boxes show sample sizes.

Reproductive success of males

Fledging success increased significantly, and the number of fledglings tended to increase with nest-building time of males

Table 1
The influence of nest-building behavior on parental decision of penduline tits (care or desert)

	Female parental decision		Male parental decision	
	χ^2	p	χ^2	p
Nest-building time	5.733	.017	0.350	.554
Carrying frequency	0.684	.408	0.010	.920
Nest age	0.137	.711	5.061	.024
Nest initiation date	0.150	.698	8.690	.003

Shows the results of two logistic regressions with backward elimination in which the dependent variable was either female or male parental decision, and nest-building time, carrying frequency, nest age, and nest initiation date were covariates (overall model fit: female decision: $\chi^2 = 5.731$, $N = 46$, $p = .017$; male decision: $\chi^2 = 8.080$, $N = 46$, $p = .018$).

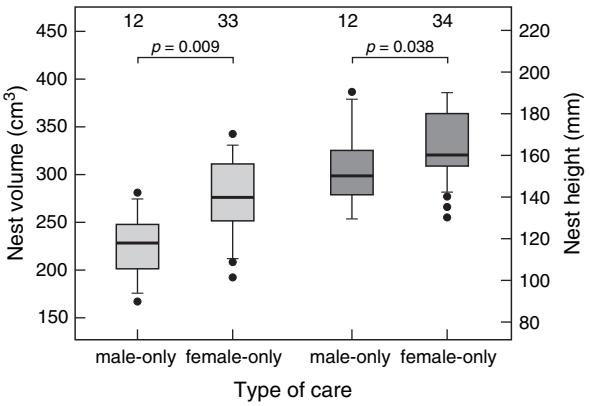

Figure 3
Relationships between nest volume (light gray boxes), nest height (dark gray boxes), and parental care decision of female and male penduline tits (see also Table 2).

(Table 3). The number of fledglings must be unrelated to nest height and volume because hatching success and the number of nestlings tended to increase with nest height and volume, but fledging success tended to decrease with these variables (Table 3). However, the statistical power of the preceding analyses was low (between 0.281 and 0.436, see Table 3). The total number of fledglings increased with both male nest-building time (Figure 4A) and nest height (Figure 4B, Table 4).

DISCUSSION

Parental decisions of males and females

Our results revealed that female penduline tits are more likely to care for broods when male nest-building time, a measure of male nest-building effort, is greater. These results are in accordance with other studies that showed that female parental effort, measured as laying date and clutch size, is positively related to male nest-building effort in black wheatears (*Oenanthe leucura*, Moreno et al., 1994) and barn swallows (*Hirundo rustica*, Soler et al., 1998). Our results also show that, in contrast to females, parental decision of males is not related to nest-building time. Therefore, we can discount the possibility that females mated to males that spent more time nest building were compelled by male desertion to care themselves, and we can reject the PCH (Witte, 1995; Wright and Cuthill, 1992). Instead, our results support the DAH, and our study is one of the few that provide evidence for preferential female parental care for offspring of males bearing certain sexually dimorphic traits (Burley, 1986; Sheldon, 2000). This female preference seems to be consistent for a given male. Males that spent more time building had a higher proportion of clutches cared for by the female over the full breeding season. We suggest that these differences in female parental effort may be explained by direct or indirect benefits that are related to nest-building time. For example, males that have abundant food at their nest sites may be able to spend more time on nest building, hence their mates may experience reduced costs of foraging and parental provisioning and benefit from higher offspring survival (e.g., Berg et al., 2005). Alternatively, good quality males (e.g., males in good condition) may be able to allocate more time to nest building, and they may sire more viable and/or attractive offspring (e.g., Evans, 1997).

Nest size was also related to parental care decisions, with tall and voluminous nests more likely to be cared for by females and deserted by males. Although nest thickness was not related to parental decisions, it was positively related to nest height. The relationship between nest size and parental decisions was consistent for a given male, and males with tall and voluminous nests had a high proportion of clutches receiving female-only care during the breeding season. Our results are consistent with the result of the study of Hoi et al. (1994), which found that nests incubated by female penduline tits were larger and thicker than nests deserted by them (i.e., incubated by males or deserted biparentally). Unfortunately, our data were not suitable to disentangle whether the relationship between parental care and nest size was driven by the male or the female because we had no data on biparentally deserted nests; in our study, when the female deserted the male always cared and vice versa. Therefore, we could not distinguish between the predictions of the PCH and the DAH with respect to nest size.

Whether males decided to care or desert was influenced by nest initiation date, and males were more likely to care if they initiated their nests later in the breeding season. This result is in accordance with the results of a previous study in a Swedish population of penduline tits, which found that the frequency of clutches with male-only care increased over the breeding season (Persson and Öhrström, 1989). The authors argued that this pattern may be due to decreased male mating opportunities later in the breeding season because many females are incubating their clutches and the operational sex ratio is heavily male biased. This seems to be a plausible explanation as the number of unmated females decreases later in the breeding season in our population as well (Szentirmai I, Székely T, and Komdeur J, unpublished data).

Table 2
The influence of nest size on parental decision of penduline tits (care or desert)

	Female-only or male-only care	
	χ^2	p
Nest height	4.288	.038
Nest thickness	3.122	.077
Nest volume	6.856	.009
Nest initiation date	0.172	.679

Shows the results of a logistic regression in which type of care (female-only or male-only) was the dependent variable and nest height, thickness, volume, and nest initiation date were covariates (overall model: $\chi^2 = 18.875$, $N = 46$, $p = .001$).

Male reproductive success and postmating sexual selection

The annual reproductive success of males (total number of offspring fledged over a breeding season) increased with nest-building time. This relationship had two components. First, males that spent a high proportion of their time building their nests had more female-only–cared clutches over a breeding season. The number of fledged offspring in turn increased with the number of female-only–cared clutches because more nestlings fledge from female-only–cared clutches than from male-only–cared clutches (Persson and Öhrström, 1989; Szentirmai I, Székely T, and Komdeur J, unpublished data). This result provides evidence for the action of postmating sexual selection on male nest-building behavior, mediated by preferential female parental effort. Second, posthatching offspring survival was positively related to nest-building behavior because fledging success increased with nest-building time. Due to higher offspring survival, there was also a positive

Table 3

The relationships between components of reproductive success in clutches with female-only care and nest-building behavior ($N = 9$) and nest size ($N = 13$) of male penduline tits

	Hatching success		Number of nestlings		Fledging success		Number of fledglings	
Independent variables	r	p	r	p	r	p	r	p
Nest-building time[a]	−.207	.541	−.250	.458	.766	.006	.543	.084
Carrying frequency[a]	.279	.405	.375	.256	−.215	.525	.189	.578
Nest height[b]	.499	.058	.397	.142	−.486	.066	−.062	.827
Nest thickness[b]	.035	.900	−.043	.879	−.262	.346	−.482	.069
Nest volume[b]	.456	.087	.557	.031	−.530	.042	−.020	.945

[a] Partial rank correlations controlling for nest age.

[b] Partial rank correlations controlling for nest initiation date.

trend between nest-building time and the number of fledglings in a given nest. Nestling survival might have increased with nest-building time because females elevated their parental effort if they mated to attractive males with high nest-building time (Limbourg et al., 2004; reviewed by Sheldon, 2000). Alternatively, offspring survival might have increased due to increased heritable viability of the offspring of attractive males (Norris, 1993; Petrie, 1994) or greater resources of attractive males, such as a food-rich nesting site (Buchanan and Catchpole, 1997; Gil and Slater, 2000).

Annual male reproductive success also increased with nest size. Males that had taller nests fledged more offspring over a breeding season. Although reproductive success was not related to nest thickness and volume, these variables were related to nest height. We argue that the positive relationship between nest size and male reproductive success is due to the high proportion of female-only–cared clutches because nest size had no direct effect on total offspring survival. This suggests that females preferentially allocated in the offspring of attractive males. These results strongly suggest that there is postmating sexual selection on nest size of male penduline tits, which is mediated by female parental care decisions.

Taken together, our results reveal the action of multiple selective forces on secondary sexual traits of the extended phenotype of male penduline tits. Previous studies have shown that nest size is involved in premating sexual selection, with males with larger nests obtaining higher mating success than males with smaller nests (Hoi et al., 1994; Schleicher et al., 1996). In addition, our results indicate that postmating sexual selection may amplify the effect of premating sexual selection. Females allocated more in the offspring of attractive males and thereby increased their reproductive success. Consequently, there is a positive interaction between the two selection forces, which may accelerate the evolution of male traits and hence has important implications for the study of sexual selection (Møller and Jennions, 2001; Møller and Thornhill, 1998). One constraint on the evolution of male nest-building behavior and nest size via postmating sexual selection is the extent to which they are genetically controlled. Our unpublished data suggest that both nest-building behavior and nest size may be at least partly genetically determined because they were repeatable for a given male (Pogány Á, Szentirmai I, and Székely T, unpublished data). We think that our results on penduline tits may apply to other species with different breeding systems as well. In species with biparental care, for example, females mated to attractive males are also

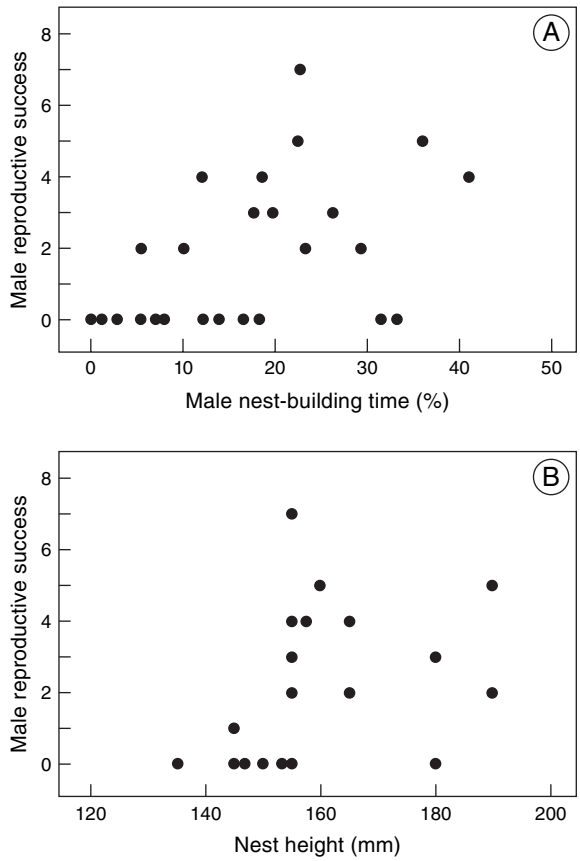

Figure 4
Relationships between (A) nest-building time (B) nest height and reproductive success of male penduline tits (see also Table 4).

Table 4

Bivariate relationships between reproductive success of male penduline tits and nest-building behavior and nest size

	Male reproductive success		
Independent variables	r	df	p
Nest-building time	.514	23	.009[a]
Carrying frequency	.108	23	.606[a]
Nest height	.467	20	.029[b]
Nest thickness	.202	14	.454[b]
Nest volume	−.112	14	.679[b]

[a] Partial rank correlations controlling for nest age.

[b] Partial rank correlations controlling for nest initiation date.

expected to increase their parental effort but, in that case, on a continuous scale (reviewed by Sheldon, 2000). However, the generality of preferential female parental effort and postmating sexual selection still needs to be tested, by investigating other suitable species in which male and female parental decisions can be distinguished clearly. If postmating sexual selection driven by differential allocation turns out to be a general phenomenon, then it should also be taken into account in models of the evolution of sexually dimorphic traits.

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